

THE IMPORTANCE OF COMMUNAL EXPERIENCE TO SURVIVAL
FOR SPIDERLINGS OF *ARANEUS DIADEMATUS*
(ARANEAE: ARANEIDAE)¹

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ABSTRACT

Outdoors, newly hatched *Araneus diadematus* spiderlings collectively inhabit a communal web until the onset of solitary orb-weaving. In the laboratory, isolated eggs hatched more frequently than grouped ones; most animals reared in isolation survived, but their mortality was greater than among communally reared controls. Spatial measurements on the communal web showed significant spreading of animals over time, an effect facilitated by low relative humidity. Animals reared in isolation subsequently built functional orb webs, though there were significant web differences between groups in protein content, size, regularity, and hub location measures. The results suggest that communal life is nonessential for hatching and growth of animals, though maturation is slower in isolates. The communal web period is discussed as flexible time which permits adjustment of ontogenetic development to varying environmental conditions.

INTRODUCTION

Most spiders, despite their diverse ecologies and intrinsic characteristics (approximately 30,000 described species, Levi and Levi 1968), undergo an early development marked by a number of common elements (Gertsch 1949, Bristowe 1939, Turnbull 1973). Among the most striking developmental features are instances of grouping by spiderlings. Soon after hatching, these immature creatures wiggle and clump considerably. They typically molt at least once within the egg sac. Postmolt gregariousness follows. Soon after that the young collectively vacate their hatching site while they carry substantial quantities of abdominal yolk.

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Generally speaking, the young of orb-weavers continue to group after leaving their birth place. Outside the egg sac these spiderlings remain together on a single web for a week or so, presumably until the yolk supply is assimilated (Bristowe 1939). Then this familial group scatters, and individuals pursue, with the exception of mating, solitary lives.

Many descriptions from McCook (1890) to Mayer (1953) support the preceding ontogenetic outline for the cross spider, *Araneus diadematus* Clerck (Levi 1971). This study examines the spatial pattern assumed when first or second instars group; it also tests the survival value of grouping behavior.

Within the laboratory, these spiderlings exhibit gregarious behavior at two periods: while inside the egg sac and after emerging onto threads jointly constructed in the sac's immediate vicinity. During the first period the hatchlings, between bouts of leg flexures and extensions, cling to one another forming pairs or larger clumps of animals. Second instars behave similarly inside the egg sac; they mass tightly into dark clumps consisting of fifty to several hundred spiderlings. Rearing experiments (solitary versus group-reared) provide evidence suggesting that grouping affects viability.

About six and one-half days after hatching, the second instars emerge upwards, laying threads as they move. This collective activity creates a sheet-like, silk structure called the communal web (Figs. 1-6) because it resembles the communal web of social spiders (Shear 1970). The spiderlings cluster peacefully on the web for about three days. Mostly they hang motionless, sometimes they touch one another, and occasionally they carry out particular thread-laying behaviors that recall movements used to weave the orb web (Witt *et al.* 1968). Several days later, coexistence between siblings gives way to aggressiveness; gnats, rejected earlier as prey, are now accepted. Then, under appropriate meteorological conditions, the animals disperse (Platnick 1976) by ballooning (dispersion through the air by means of silk threads), and individuals become solitary orb weavers.

The gregariousness seen on the communal web is examined from two perspectives. First, isolation experiments look into the relevance of communal web experience in the development of solitary web-building behavior. Second, the nature of the spiderlings' spatial arrangement while on their common web, and its variation over time, are analyzed by the nearest neighbor method (Clark and Evans 1954). Also, the hypothesis is tested that humidity significantly influences the spatial arrangement; this conjecture seems attractive because animals with high surface-to-volume ratios usually have problems with water balance (Cloudsley-Thompson 1962).

MATERIALS AND METHODS

Rearing Experiments.—Spiderlings (*Araneus diadematus* Cl.) were reared from egg sacs obtained from Upstate New York (Mr. Leonard Pankhurst, 204 Stroud Street, Canastota, N. Y.). Egg sacs not used immediately were stored in a refrigerator at 7°C for periods of one to two months. An egg mass was prepared for experimentation by removing it from the sac and separating it completely into individual eggs. These eggs were incubated in high ambient humidity (above open water pans) while automatic temperature and light control simulated a 16 hr day and 8 hr night. From January through July, daily maximum temperatures averaged 25.9±1.7°C (SD); nightly minimums averaged 21.9±1.3°C.

Some of the eggs separated from a given egg mass were raised in isolation; the remainder were reared communally. An egg (chosen at random) was isolated by placing it alone on a tuft of cotton situated at the bottom of a 5.0 ml screw-top glass vial, then loosely twisting the cap in place. Communal eggs were housed together on cotton inside a similar vial. Both groups were kept under the environmental regimen mentioned earlier until the animals in the communal group moved upward; ascension signalled the onset of communal web construction.

For each treatment group, these observations were recorded and tabulated: eggs hatched, eggs not hatched; live first instars, dead first instars; live second instars, dead second instars. Five egg masses were individually analyzed in this fashion. The association between the rearing conditions and the viability of a developmental stage was tested by using a two-way contingency table (Sokal and Rohlf 1973).

Isolation Experiments.—The first of two experiments, in February, used an egg sac containing 700 eggs; the second, in March, used a sac with 507 eggs. Each egg sac was dissected; some of its eggs were reared singly, the remaining ones together, as the previous section described.

In experiment one, three treatment groups were set up by selecting animals raised in either the communal or the isolated manner. At the onset of communal web formation,

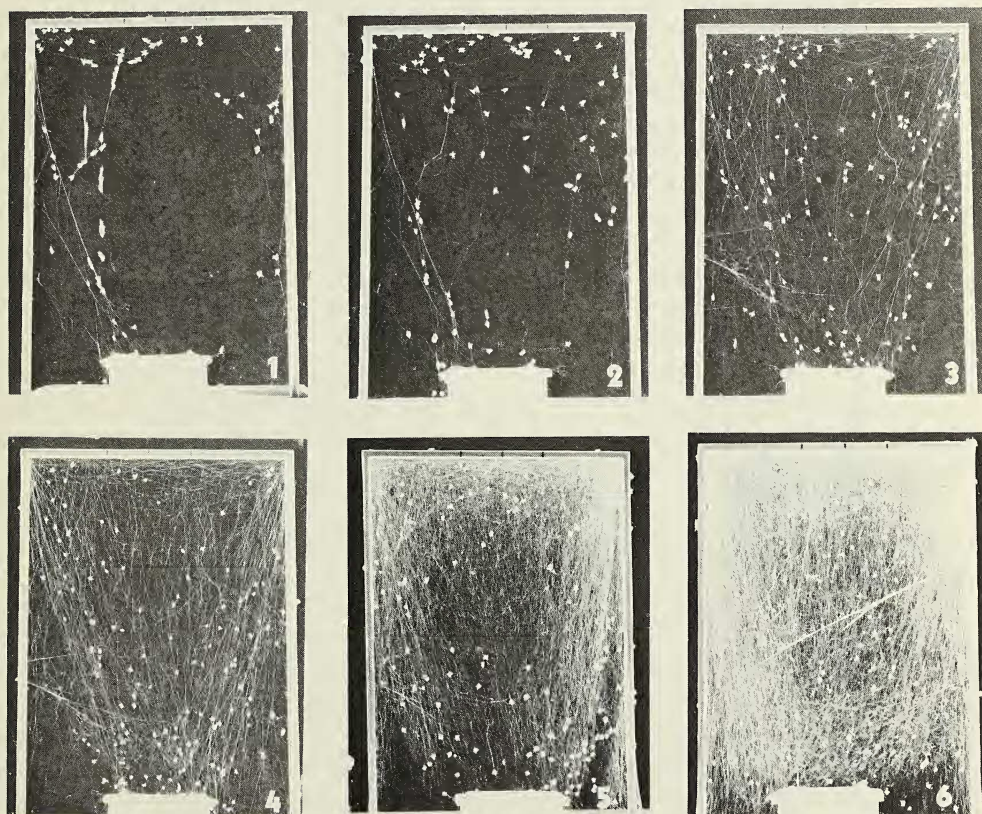


Fig. 1-6.—Time series showing construction of communal web by *Araneus diadematus* spiderlings: 1, 30 sec; 2, 60 sec; 3, 5 min; 4, 25 min; 5, 5 hr; 6, 24 hr. Spiderlings show up as white dots, silk as white lines. Calculations have shown that the spatial pattern changes over time. The rectangular frames are 13 cm wide and 18 cm high.

30 spiderlings were taken in haphazard fashion from the animals reared communally; each was moved to a wooden frame (18x13 cm, hwx) and individually contained in a translucent, polyethylene pail sealed by a snap-on cover. These animals composed the precommunal group—a name stressing their lack of experience in both constructing and inhabiting the communal web. The remainder of the spiderlings raised in the communal fashion were collectively released onto a single frame to build the communal web, and were kept together in a polyethylene pail for four days; 50 of these animals (the communal group) were randomly selected and housed singly. The third group was comprised of 50 isolated spiderlings (the isolated group). These animals were taken from their vials and likewise individually housed.

Isolated and communal treatment groups were also established in experiment two. A third group was set up too: the confined isolate group. These were animals reared in isolation and confined in their vials during the interim of four days when communal animals coexisted on common threads. Fifty such spiderlings were chosen and individually housed as before.

The webs of each group member were photographed daily (Fig. 7). Web measures were calculated from photographs of the second web constructed by each spiderling. The calibration of these photographs and the derivation of the 25 web measures have been previously described (Witt *et al.* 1968).

Web measures evaluated the size, fine structure, regularity, and shape of the web. Size measures (number of radii; median angle; number of spirals, West, North, East, and South; spiral area; center area; frame area; thread length) reflected the spatial extent and number of thread elements. Three fine structure measure (mesh width; median mesh size, North and South) expressed the density of threads in the spiral area. Nine regularity measures (oversized angles; standard deviation of central angles; angle regularity; relative deviation of spiral turns, West, North, East, and South; standard error of median mesh size, North and South) assessed the variability of thread placements. Variations in the elliptical form of the web and in the symmetry of hub location were detected by three shape measures (width over length; radius North over South; radius East over West). All these measures are defined in Witt *et al.* (1968).

Non-geometrical data were also collected in experiments one and two. The micrograms of protein in a spiderling's second web was determined using the method of Lowry *et al.* (1951). The time elapsed in days between the placement of an animal in its polyethylene pail and the fabrication of its first web was recorded.

After containment in a polyethylene pail, a spiderling was fed a gnat (*Hippelates pusio*) in its first web, and afterward in alternate webs. Water was sprayed as a fine mist into the pail every other day.

For each isolation experiment, the 27 measurements (web measures and non-geometrical data) made on all second webs were used to construct a lower triangular correlation matrix (Burch 1977). These two matrices were individually analyzed by factor analysis: each correlation matrix was factored by a principal component analysis (Harman 1967); next the resultant principal component matrix was orthogonally rotated according to Kaiser's varimax criterion (Kaiser 1958). The rotation produced a factor matrix: a set of columnar factors. The number of factors retained in the matrix was decided by the eigenvalue-one rule (Rummel 1970). Pooling the data from both experiments for a single factor analysis was avoided because: a) the treatment regime between experiments was different; b) a period of one month passed from the start of the first experiment to the

start of the second. Calculations of the factor analyses were carried out on computer programs developed by John Sall (Barr *et al.* 1975).

Factor analysis served two purposes. First, it clarified the complex interrelationships among the 27 web measurements—in the factor matrix, each factor was correlated with and so could be interpreted as a distinctive pattern of the original measurements. A measurement whose factor loading (correlation coefficient between measurement and factor) exceeded an absolute value of 0.32 was judged important for interpretative purposes; in such a case, the factor accounts for more than 10% of the measurement's variance. Second, it simplified the data by reducing a large number of correlated web measurements to a smaller number of uncorrelated variables (the factor scores). A spiderling's second web could then be described by factor scores instead of the correlated measurements. These scores were calculated by the method of regression (Rummel 1970).

If two factors from different experiments showed similar patterns of correlation with the original measurements, they were compared through the coefficient of congruence

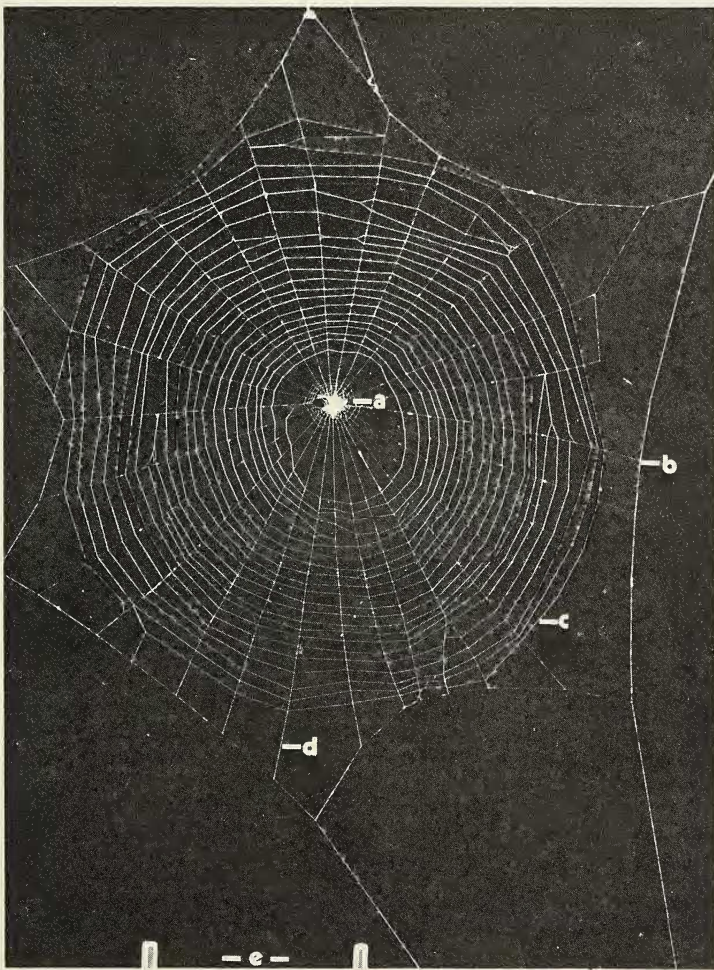


Fig. 7.—Typical orb web identifying principal constituents: hub(a), frame(b), spiral(c), radius(d), standard measuring 20 mm between prongs(e).

(Harman 1967). It measures not only pattern similarity but also magnitude similarity, and behaves like a correlation coefficient ranging from -1.00 (for perfect negative similarity) through zero (for complete dissimilarity), to 1.00 (for perfect similarity).

For each factor, a univariate analysis of variance (Sokal and Rohlf 1973) was performed on the factor scores to test the null hypothesis that the means of the treatment groups were equal. If the null hypothesis was rejected, the Least Significant Difference (LSD) method of multiple comparison (Snedecor and Cochran 1967) detected which pair(s) of means differed significantly.

Spatial Pattern Experiments.—Ten egg sacs were used in the spatial analysis. Each was prepared for observation by the method described for rearing communal spiderlings. When communal web formation seemed imminent for a given egg mass, the emergent spiderlings were permitted to fabricate this structure on the standard rectangular frame. Web and inhabitants were confined at that time in a polyethylene pail and afterwards were carefully removed at 24 hr intervals for web photography (Witt *et al.* 1968). Photographs were taken over a four day period. The number of spiderlings on a given web ranged from 10 to 500.

Nearest-neighbor distance for each spiderling was evaluated from 35 mm negatives. A negative was inserted into a slide projector, shown against a grid background whose square of unit size measured 1 mm along an edge, and enlarged to twice life size. An animal's location was recorded in Cartesian coordinates; these coordinates were analyzed by a computer program whose output included the nearest-neighbor distance for each animal.

Establishing the position of a spiderling in such a two dimensional coordinate system presupposes that the communal web exists in a single plane. Compelling the emerging animals to moor their threads to the planar wooden frame insures that the resulting web conformation approximates this desired planarity.

The distance between an individual and its nearest neighbor provides the basis for a measure of spatial pattern. A set of such distances was measured from the daily photograph of a given spiderling group; from this the mean nearest neighbor distance was calculated. The mean nearest neighbor distance expected if the members of this group were randomly distributed was also computed; Clark and Evans (1954) have shown this value to be $1/2\sqrt{\rho}$ where ρ is the density of the observed distribution expressed as the number of individuals per unit of area. The ratio of the observed mean distance to this expected mean distance, known as the R ratio (Clark and Evans 1954), evaluated spatial pattern: it assumes values less than 1 for aggregated populations, the value 1 for a random arrangement, and values greater than 1 in uniform populations.

A two-factor analysis of variance was calculated using the R values. The factors investigated were time (days 1-4) and spiderling group size (large, 50 animals or more; small, less than 50 spiderlings). In this analysis of variance model, time was considered a within-subjects variable, and spiderling group size a between-subjects variable (Myers 1972).

Humidity Experiments.—Inside a number of rectangular glass chambers (102x102x203 mm, lxwxh), a series of discrete relative humidities was maintained through saturated salt solutions; the salt solutions used and the relative humidities produced at 22°C (Winston and Bates 1960) were: LiCl · H₂O, 12.3%; MgCl₂ · 6H₂O, 32.8%; Na₂Cr₂O₇ · H₂O, 53.9%; NaCl, 75.8%; Pb(NO₃)₂, 96.4%. These particular salt solutions afford the advantage that their associated humidities are invariant over a considerable temperature range. Humidities were verified using the salt deliquescence method (Winston and Bates 1960).

Square screen platforms (90x90 mm) resting on four pieces of polyethylene tubing, one heat-fused at each corner, supported balsa wood frames (115x75 mm, hwx) above the level of salt solution in each container. Having lived on their communal web for one day, individual spiderlings from a single egg sac were haphazardly chosen and randomly assigned to one of the five humidity chambers until each contained 30 animals. The top of every chamber was then sealed airtight; after 18 hr the animals on their webs were photographed through the glass. Kodak Plus-X film was used. The entire experiment was repeated with the offspring from another egg sac.

Nearest-neighbor analysis and the R index were employed to describe the spatial pattern at each relative humidity. The trend of R values over humidity was tested for significance (Cooper 1975).

RESULTS

Rearing Experiments.—For most cocoons, the isolated eggs hatched in higher percentage than their communal counterparts did. However, the percentage of surviving first and second instars was generally lower among isolated animals than among the corresponding communal group. These results are shown in Table 1.

Statistical tests showed a significant association between the rearing conditions and the viability of specific developmental stages. Using additive data over all egg masses, a two-way contingency table classified eggs according to whether they hatched or not, and also by treatment. These data indicate that isolated eggs were more successful at hatching than their communal counterparts ($\chi^2=27.7$, $P<0.001$, $df=1$). A similar table tabulated the survival of the first and second instars with their treatments; isolated spiderlings died more frequently than communal animals did ($\chi^2=16.6$, $P<0.001$, $df=1$).

Isolation Experiments.—The resultant factors and their loadings are shown for isolation experiments 1 and 2 respectively in Tables 2 and 3. In experiment 1, seven

Table 1.—Differences between isolated and communal treatments in the viabilities of eggs and spiderlings. In most cocoons, the percentage of isolated eggs that hatched was greater than the percentage of communal eggs that hatched. Conversely, communal spiderlings generally survived in higher percentage than isolated spiderlings survived. Cocoons are specified by uppercase letters. The values in parentheses are the percentages of nonviable organisms to the total observed for the given treatment and developmental stage. The data headed "spiderlings" are additive for first and second instars.

Cocoon	Treatment	Eggs		Spiderlings	
		Hatched	Not Hatched	Live	Dead
A	Communal	382	5(1.3)	382	0(0.0)
	Isolated	115	5(4.2)	109	6(5.2)
B	Communal	33	804(96.1)	28	5(15.2)
	Isolated	7	93(93.0)	7	0(0.0)
C	Communal	164	504(75.4)	163	1(0.6)
	Isolated	24	115(82.7)	24	0(0.0)
D	Communal	200	367(64.7)	198	2(1.0)
	Isolated	57	63(52.5)	55	2(3.5)
E	Communal	68	662(90.7)	49	19(27.9)
	Isolated	16	94(85.4)	3	13(81.2)

Table 2.—From the data of isolation experiment 1, seven factors were calculated through principal components then rotated by the varimax criterion. Factors are named in the text. Variance extracted is the percent of total variance in the data removed by a specific factor. Communality is the proportion of a measurement's variance accounted for by all factors. Abbreviated: No-Rad=number of radii; Med-Ang=median angle; Spiral-W, -N, -S, -E=number of spirals West, North, South, East; Spiral=spiral area; Center=center area; Frame=frame area; Thread=thread length; Os-Ang=oversized angles; SD-C=Ang=standard deviation of central angles; Ang-Reg=angle regularity; Dev-Sp-W, -N, -E, -S=relative deviation of spiral turns West, North, East, South; Msh-SE-N, -S=standard error of median mesh size North, South; Mesh-Wdh=mesh width; Mesh-N, -S=median mesh size North, South; Wdh-Lgth=width over length; Rad-N-S=radius North over South; Rad-E-W=radius East over West; Protein=micrograms of protein in second web; Time-2=time elapsed before construction of second web. Loadings greater than or equal to an absolute value of 0.32 are shown in parentheses.

Factors:	1	2	3	4	5	6	7	
Variance extracted:	25.9	10.4	9.9	6.6	7.3	11.8	5.0	Total=76.9%
Web measurements	Factor loadings							Communality
No-Rad	(.80)	.13	(-.38)	.11	-.12	-.21	-.05	.88
Med-Ang	(-.76)	-.19	.31	-.20	.20	.26	.08	.87
Spiral-W	(.81)	-.05	-.07	(.46)	-.01	-.01	-.05	.88
Spiral-N	(.88)	-.12	-.07	.10	.11	-.13	.20	.87
Spiral-S	(.92)	-.10	-.10	-.08	-.02	-.04	-.21	.92
Spiral-E	(.88)	-.17	.01	.13	.13	-.02	.02	.85
Spiral	(.84)	(.34)	-.10	.04	-.12	(.32)	-.10	.95
Center	(.44)	.15	-.25	-.00	(-.47)	(.41)	-.15	.69
Frame	-.06	.31	.14	.12	(-.67)	.12	-.03	.60
Thread	(.96)	.09	-.13	.10	-.09	.13	-.08	.99
Os-Ang	.11	.15	(.80)	-.03	-.18	-.18	.20	.78
SD-C-Ang	(.42)	-.05	(.84)	-.12	.01	.05	-.07	.91
Ang-Reg	(-.39)	-.09	(.87)	-.07	.02	.03	-.01	.92
Dev-Sp-W	.25	(.67)	-.02	-.07	-.06	.14	.06	.54
Dev-Sp-N	-.03	.30	.27	-.28	(-.60)	.22	.17	.69
Dev-Sp-E	-.06	(.69)	.02	.06	-.14	.14	-.11	.53
Dev-Sp-S	-.05	(.76)	-.03	.04	-.09	.19	-.10	.63
Msh-SE-N	-.31	(.32)	.16	-.25	(-.43)	(.54)	.10	.77
Msh-SE-S	(-.43)	(.45)	.04	.17	.13	(.39)	.12	.59
Mesh-Wdh	.03	(.58)	.05	-.00	-.18	(.73)	-.13	.93
Mesh-N	-.07	.12	-.03	-.07	-.14	(.84)	.03	.76
Mesh-S	.03	.25	-.08	-.09	.08	(.85)	-.03	.80
Wdh-Lgth	.14	.09	-.02	(.81)	.16	-.17	-.04	.74
Rad-N-S	-.08	-.21	.10	.05	-.21	.09	(.86)	.85
Rad-E-W	.19	.00	-.12	(.70)	-.14	-.00	-.01	.56
Protein	.17	-.10	-.01	.31	(-.35)	.29	(-.56)	.65
Time-2	-.30	.27	.24	-.04	(.55)	.29	-.13	.62

uncorrelated factors accounted for 76.9% of the variance in the 27 web measurements. Eight factors explained 80.8% of the data's variance in experiment 2.

The tables also list, for each web measurement, the proportion of its variance that is explained by the factors removed. The explained variance of a measurement is called its communality. Among all variables, the variation in thread length was the one most completely described by each factor set; least explained were relative deviations of spiral turns East in experiment 1 and frame area in experiment 2.

A particular factor generated from the data of one experiment often resembled in its pattern and magnitudes of loading a factor or factors generated from the data of the

other. Therefore the naming and interpreting of similar factors can economically be discussed together rather than piecemeal.

In both factor analyses, each of the first factors loaded positively on the measures of web size. The coefficient of congruence (symbolized by the Greek letter delta) between the two was high ($\delta=+0.95$). So they were given the same name: 'web size' factor. Presumably such a factor represents the number of filamentous components in the web.

As shown in the factor matrix of the first experiment, factor 2 was associated with measurements of web regularity and factor 6 with measurements of fine structure. The three largest coefficients of factor 2 were linked to the regularity of spiral placement—relative deviation of spiral turns South, East, and West (loading on this measure in the North almost reached criterion). Factor 2 was called 'spiral irregularity'. The major loadings of factor 6 were on the three measurements of fine structure (mesh width; median mesh size, North and South). In addition, this factor showed substantial association with the standard error of median mesh size, North and South. Accordingly, it reflected 'mesh size and irregularity'.

Factor 2 in the matrix of the second experiment appeared to be a composite of both regularity and fine structure measurements. As expected, it resembled the 'mesh size and irregularity' and the 'spiral irregularity' factors, its respective coefficient of congruence with each being $+0.74$ and $+0.72$. This factor was named 'mesh size and spiral irregularity'.

Factor 3 of experiment 1 loaded distinctly on the three measurements concerned with the regularity of radial thread arrangement (oversized angles, angle regularity, and standard deviation of central angles). It revealed a striking likeness to factor 4 of experiment 2 ($\delta=+0.82$). Both factors were named 'central angle irregularity'.

Measurements of web shape dominated the loadings in factor 4 of experiment 1. The coefficients of this factor in diminishing rank were width over length, radius East over West, and number of spiral turns West. These are all measurements of web symmetry, viz., as it regards hub location. Factor 4 was called 'hub symmetry'. Except for sign reversals, it was similar to factor 8 of experiment 2 ($\delta=-0.72$), and so the latter entitled 'hub asymmetry'.

Showing little similarity to any factor of the second experiment, factor 5 from experiment 1 displayed a confusing mixture of coefficients. It was characterized by large negative loadings on two size measurements, frame and center areas, by negative loading on two regularity measurements, relative deviation of spiral turns North and standard error of median mesh size North, by a positive association with time before web construction, and by a negative loading on the protein content of the web. This factor was labeled 'time-associated size and irregularity diminution' and probably reflected web changes caused by malnutrition in spiderlings who delayed the onset of orb weaving.

Factors denoting the vertical and lateral location of the web's hub were discovered in both factor analyses. Factor 7 of experiment 1 loaded in bipolar fashion: positively with radius North over South, and negatively with protein content of the web. It was named 'vertical hub symmetry vs. protein'. Factor 3 of experiment 2 resembled factor 7 ($\delta=+0.66$); it differed from factor 7 by failing to show a large inverse relationship with protein contained in the web, and was therefore dubbed 'vertical hub symmetry'. Another factor from experiment 2, factor 6, showed some likeness to the 'vertical hub symmetry vs. protein' factor ($\delta=+0.36$). Having loaded positively on both radius East over West and frame area, and negatively on the protein content of the web, it was named 'lateral hub symmetry vs. protein'.

Table 3.—The factor matrix for the data of isolation experiment 2 comprised eight factors. Details are explained in Table 2.

Factors:	1	2	3	4	5	6	7	8	
Variance extracted:	28.2	15.0	5.1	6.4	7.1	4.4	9.1	5.5	Total=80.8%
Web measurements	Factor loadings								Communality
No-Rad	(.91)	-.23	-.01	-.02	-.02	-.01	-.01	-.08	.89
Med-Ang	(-.89)	.17	.01	-.02	.91	-.04	.01	.13	.83
Spiral-W	(.84)	-.26	.09	-.07	.11	.06	.12	-.13	.84
Spiral-N	(.80)	(-.33)	.12	-.10	.20	-.03	.25	.07	.88
Spiral-S	(.81)	-.10	-.23	-.03	-.10	-.07	(.43)	.13	.93
Spiral-E	(.81)	-.23	-.05	-.12	.04	-.04	(.40)	-.04	.88
Spiral	(.87)	.30	-.09	.03	.23	-.07	.01	-.08	.93
Center	(.34)	.03	.02	.06	(.76)	-.17	-.08	-.02	.74
Frame	-.05	(.63)	-.08	-.01	.23	(.34)	.06	-.02	.57
Thread	(.95)	-.00	-.07	-.01	.19	-.06	.18	-.02	.97
Os-Ang	.02	-.01	-.00	(.92)	-.08	.03	-.01	-.10	.86
SD-C-Ang	(-.67)	.27	-.04	(.58)	-.04	.07	.03	.02	.87
Ang-Reg	(-.64)	.25	.06	(.60)	.01	.05	.06	.04	.86
Dev-Sp-W	.04	(.57)	(-.34)	.01	-.14	.13	-.20	(-.49)	.76
Dev-Sp-N	-.14	(.79)	.28	-.12	-.14	.04	-.16	.28	.86
Dev-Sp-E	-.15	(.56)	-.09	.16	.02	-.22	(-.49)	-.03	.66
Dev-Sp-S	-.15	.22	-.27	-.06	-.01	.12	(-.78)	.06	.78
Msh-SE-N	(-.42)	(.75)	.18	.07	-.10	.01	-.18	.15	.83
Msh-SE-S	-.28	.18	.08	-.03	.17	.16	(-.83)	.08	.84
Mesh-Wdh	-.14	(.83)	-.16	.10	.27	-.13	-.30	-.14	.94
Mesh-N	-.26	(.65)	.01	.19	.24	-.24	-.05	-.03	.64
Mesh-S	-.04	(.32)	-.09	-.15	(.75)	-.09	-.26	-.10	.78
Wdh-Lgth	.13	-.09	.02	.08	.04	-.02	.13	(-.90)	.87
Rad-N-S	-.10	.03	(.93)	.01	-.00	-.03	.12	.01	.89
Rad-E-W	(.35)	.00	.18	.01	-.12	(.58)	-.24	(-.37)	.70
Protein	(.34)	.04	.13	-.09	.08	(-.67)	.02	-.10	.61
Time-2	-.23	.06	-.13	.12	(-.57)	-.27	(-.33)	-.23	.64

Two factors of experiment 2 described time-dependent changes in web structure; various details of size became smaller and of fine structure irregular when the spiderling postponed the fabrication of its web. Factor 5 was characterized by positive coefficients associated with center area and median mesh size South (mesh-S), and a negative loading on time elapsed before web construction. It was subsequently termed 'time vs. center and mesh-S'. The three largest loadings of factor 7, all negative, were: standard error of median mesh size South, and relative deviation of spiral turns South and East. This factor also correlated positively with the number of spiral turns South and East, and inversely with time elapsed before web construction. It was recognized as 'time vs. spiral regularity, South and East'.

For each factor, a statistical summary (N , \bar{x} , $SD_{\bar{x}}$) of its scores, by treatment, together with the results of a univariate analysis of variance, across treatments, is presented in Table 4. Significant F-ratios ($P < 0.05$) were detected in two factors of experiment 1: 'spiral irregularity' and 'vertical hub symmetry vs. protein'. In experiment 2, 'mesh size and spiral irregularity' when tested gave a significant F-value.

A posteriori comparisons of the treatment groups for the three preceding factors uncovered these differences. Regarding 'spiral irregularity', the isolated animals built webs

that were more regular in the placement of spiral threads than were the webs built by their communal counterparts. Scores on the 'vertical hub symmetry vs. protein' factor showed two things. First, isolates constructed webs containing less protein than webs constructed by communal or precommunal animals. Second, they situated the hubs of these webs more centrally along the vertical axis than the hubs situated by spiderlings of the other groups. Finally, analysis of the results from the 'mesh size and spiral irregularity' factor revealed that the confined isolates wove webs with greater regularity in spiral placement and with smaller mesh size than seen in the webs of their isolate or communal counterparts.

Spatial Pattern Experiments.—The spatial patterns taken by large groups of spiderlings did not differ from the patterns taken by small groups ($F=1.94$, $df=1$, N.S.). And group size and time did not interact significantly ($F=1.59$, $df=3$, N.S.). The arrangement in space of a group of spiderlings changed, however, over time ($F=5.64$, $df=3$, $P<0.005$). For each day, the R values from the two sizes of groups were pooled, and the mean was calculated. Mean R values for days 1-4 were respectively: 0.756, 0.860, 0.934, 0.957. Over this series of values, Cooper's test (1975) for increasing trend was significant ($P<0.02$): the spiderlings drew apart from one another over time, moving from an aggregative towards a random arrangement.

Humidity Experiments.—For humidities 12.3% through 96.4%, the respective R values are shown below; each series corresponds to an experimental replication: 0.780, 0.747, 0.640, 0.706, 0.539; 0.599, 0.452, 0.512, 0.374, 0.300. Animals aggregated at all humidities. Trend tests (Cooper 1975) performed on each data set were significant ($P<0.015$). R values decreased as humidity increased, i.e., the spiderlings drew together when the humidity went higher.

DISCUSSION

Several hypotheses can explain why isolated eggs showed a lower mortality than communal eggs showed. An inviting hypothesis posits the influence of a contagious factor, e.g., a pathogenic microorganism (Cloudsley-Thompson 1968) that spreads through the communal context. Another explanation is supported by two pieces of circumstantial evidence: 1) the second instar spiderlings within the egg sac were sometimes seen to clutch unhatched ova; 2) second instars emerging from the egg sac were often visibly different in their sizes. These observations imply that second instars could have fed on unhatched ova; Valerio (1974) describes the occurrence of this phenomenon among second instars of the American House Spider (*Achaearanea tepidariorum* Koch). Or possibly the high mortality of communal eggs resulted simply from overcrowding. However, females of *Araneus diadematus* Clerck normally lay their egg sacs in cramped surrounding, e.g., out-of-the-way crevices beneath peeling bark (McCook 1890), where conditions of space, ventilation, and humidity could be more harmful than those in the laboratory.

Probably nowhere is isolation more drastic in consequence than among the social insects; hive-bees, ants, and termites, when isolated, survive only a few hours, or at most a few days (Chauvin 1967). My study showed that the spiderlings could be reared in isolation in the laboratory, but it also pointed out a statistical association between viability and rearing condition.

Why did isolated spiderlings die more frequently than communal spiderlings did? Since this question was not examined directly by experiment, its answer can only be speculated

Table 4.—Descriptive statistics, Least Significant Difference tests (LSD), and Analysis of Variance (ANOVA) for the factor scores of the first (1) and second (2) isolation experiments. Factors are listed in the order of discussion under RESULTS. Scores for a given factor were collectively standardized to a mean of 0.5 and a variance of 1.0. No significant difference ($P < 0.05$, LSD test) exists between means labeled with the same symbol (*, #). Abbreviated: \bar{x} =mean; $SD_{\bar{x}}$ =standard error. The number of spiderlings (N) in the treatment groups were confined isolate, N=43; communal, N=37; precommunal, N=40; precommunal, N=28.

Factors	Experiment	Treatment Groups						ANOVA	
		Confined Isolate	Isolate	Communal	Precommunal	F value	Prob>F		
Web size	1	—	0.46	0.37	0.74	1.14	0.32		
	2	—	0.179	0.154	0.167	1.79	0.17		
Spiral irregularity	1	0.32	0.77	0.49	—	3.68	0.03		
	2	0.158	0.172	0.164	0.38* #	0.80	0.06		
Mesh size and irregularity	1	i13,—	0.24 *	0.82 #	0.180	2.80	0.06		
	2	—	0.168	0.148	0.217	3.66	0.03		
Mesh size and spiral irregularity	1	—	0.23	0.54	—	0.41	0.67		
	2	—	0.123	0.164	0.47	0.22	0.81		
Central angle irregularity	1	0.19 #	0.74 *	0.67 *	—	1.32	0.27		
	2	0.155	0.188	0.145	—	0.46	0.64		
Hub symmetry	1	—	0.62	0.41	0.221	1.37	0.26		
	2	0.48	0.156	0.145	—	3.37	0.04		
Hub asymmetry	1	0.159	0.42	0.58	—	0.10	0.90		
	2	—	0.171	0.170	0.70	1.30	0.28		
Time-associated size and irregularity diminution	1	—	0.30	0.54	0.164	2.60	0.08		
	2	0.61	0.174	0.160	—	1.45	0.24		
Vertical hub symmetry vs. protein	1	0.185	0.42	0.43	—	0.46	0.64		
	2	—	0.160	0.132	—	1.37	0.26		
Vertical hub symmetry	1	—	0.41	0.70	0.33	0.10	0.90		
	2	—	0.148	0.158	0.205	1.30	0.28		
Lateral hub symmetry vs. protein	1	—	0.83 *	0.38 #	0.24 #	2.60	0.08		
	2	0.50	0.133	0.161	0.208	1.45	0.24		
Time vs. center and median mesh size South	1	0.160	0.44	0.55	—	0.46	0.64		
	2	—	0.170	0.171	—	1.37	0.26		
Time vs. spiral regularity South and East	1	0.69	0.40	0.35	—	0.10	0.90		
	2	0.157	0.175	0.164	—	1.30	0.28		

on. Others have noted the same phenomenon. Darchen (1965) reared social spiderlings (*Agelena consociata* Denis) in isolation and observed that these animals died sooner than did group-reared young; he attributed their reduced longevity to the absence of either inter-individual contacts or trophallaxis. Studying the same spider, Krafft (1971) made similar findings. His isolated animals did not live so long or grow so large as animals that were reared in groups. In my study, the most noticeable behavior of grouped animals inside the cocoon was their frequent touching of one another. Whether such tactile stimulation can account for the difference in viabilities should be tested.

The calculations of the factor analyses made possible an economical and concise description of the structure of the orb web. Generally speaking, the generated factors described a web in five ways. Classifications a) through e) progress from the most important to the least important in explaining the variance of the experimental data: a) overall size: the total number of filamentous segments in the web (or possible the sum of the quadrilaterals that make up the catching zone); b) mesh size and its variation (a mesh is the trapezoid shape formed by two adjacent radii and two adjacent spirals); c) irregularity of spiral thread placement; d) irregularity of radial thread placement (another way of saying 'central angle irregularity'); e) the lateral and vertical symmetries of the hub. Witt and Reed (1965) made a less detailed factor analysis of some of the 27 web measurements. They also identified factors related to web size, mesh width, and hub symmetry.

As the factor scores from the isolation experiments showed, the second orb webs woven by isolates were not very different in their geometry (and possible function) from similar structures built by their communal litter-mates. Because the isolates neither constructed nor occupied the communal web, such experience can be judged unnecessary for the development of normal orb-weaving behavior. This developmental homeostasis (Mayr 1974, Alcock 1975) would seem advantageous to the short-lived spider, for whom, early in life, the orb web is essential to secure prey.

The physiological basis of such development probably resides in the maturation of the central body. This structure is a flat neuropilar sheet that stretches across the posterior part of the spider's brain. Babu (1975) found a correspondence in time between the formation of the central body and the start of orb-weaving behaviors in the second instar.

Other workers have performed isolation experiments. Petrusiewiczowa (1938) and Mayer (1953) isolated spiderlings *after* their communal web association, and reared them in small tubes that prevented web-building behavior. When released, these animals constructed seemingly normal webs on their first attempt. Using a similar experimental approach, Witt *et al.* (1970) found that spiders confined in narrow glass tubes after the communal web phase, and then released for several days afterwards built webs whose size measures (thread length, spiral area, numbers of radii and spiral turns) were significantly less than those of the control group; these size measures could be brought to control levels by a preliminary pulling of thread that partially emptied the spider's silk glands. This diminution was not observed in the webs of my solitary animals, probably because my confinement period was shorter and less restrictive.

The primary geometrical difference distinguishing the webs of solitary from group-reared animals was the solitary spiders' greater regularity in spiral thread placement, through secondary differences also included their more central hub location and smaller mesh size. All of the above web measures change progressively as a spider ages (Witt *et al.* 1968, Witt *et al.* 1972, Risch 1977): spiral placement becomes more irregular, hub location more asymmetric, and mesh size increases. Interpreted in this context, one

might say that the spiderlings reared in groups matured more rapidly than the isolates matured.

These 'group effects', as they influence viability and maturation, are commonplace among the insects (Chauvin 1967, Cotter 1974). In spiders, Krafft (1971) observed that 'group effects' among the young of the communally living spider *Agelena consociata* resulted in a reduction of the intermolt period and a growth acceleration.

Because the treatment effects in the isolation experiments were minor, the factor analysis can be interpreted from yet another perspective. It suggests what elements natural selection might modify to adapt the spiderling to a changing environment. Of the five classes of factors, those associated with overall web size and with mesh size represented the two greatest sources of variation observed in the second webs of spiderlings. Those associated with irregularity in thread placement and with hub symmetry accounted for smaller sources.

Witt and Ralings (1973) have calculated heritabilities (broad sense) for some of the 27 web measurements from the cross spider. Their values of heritability paralleled the levels of phenotypic variation in the five classes of factors. All size measurements—radii number, number of spirals in the four cardinal directions, frame area, spiral area, center area, and thread length—showed high heritabilities (they were under strong genetic control). The heritabilities of measurements of mesh size were significantly different from zero but about half as large as those for measurements of web size. Finally, there was little or no evidence of genetic control for those web characteristics measuring the irregularities of thread placement and those measuring the symmetry of the hub.

Both kinds of information, phenotypic variation and heritabilities, suggest which web structures natural selection is most likely to modify. It seems to be placing a premium on varying web size and mesh size to adapt the spiderling to a changing environment. But it tolerates little variation in the irregularity of thread placement and in hub symmetry. Risch (1977) reached similar conclusions about the evolution of the web of the adult cross spider.

Finally, the factors have two potential meanings for the biology of the spider. But both need independent confirmation. The first is related to the most obvious purpose of the web for the spiderling: catching prey. Could these factors be important elements in making the web an efficient trap? Some evidence supports them in this role.

Witt *et al.* (1968) argued that web and mesh sizes are important in prey capture. A larger web covers a wider area in which flying insects can get caught. Mesh size limits the size of prey that the web can trap: insects that are too large or too small escape. For the catching zone to be effective at all points, reason suggests that the placement of spirals must be regular. Regular arrangement is also necessary for radial threads because they provide the only avenues for the spider to approach and retrieve prey from the catching zone. Finally, the location of the hub within the web can determine how fast the spider gets to its potential prey. For example, will the spider's approach be assisted or hindered by gravity, and over what fraction of the spiral area will its approach be assisted or hindered?

A second potential meaning of factor analysis for the biology of the spider is understanding the internal organization of web-building behavior. A given factor has high loadings for a number of behavioral measurements. If independent evidence also suggests that these same measurements are related to one another and possibly to common internal causes, then the factor could represent an internal organization of behavior (e.g., a neural structure) common to each of these measured behaviors (Huntingford 1976).

Factors that describe web size and those that describe regularity of thread placement hint at the existence of respective internal centers for these behaviors. Support is two-fold. Comparative histological studies have revealed that the central body of the brain is a neural center important in the operation of web-building behavior (Bullock and Horridge 1965). Witt *et al.* (1964) made random lesions in the brains of cross spiders. Some of these animals built webs smaller in size than webs built before treatment; others wove webs similar in size to control webs but altered in regularity.

Nearest-neighbor measurements made during the spatial pattern experiment provided mathematical support for the spiderlings' aggregation on the communal web. Whether the spiderlings group together because of an interattraction between individuals or through the influence of extrinsic conditions, remains a fine distinction not resolved by these experiments. Since homogeneous surroundings were provided for the spiderlings, and because the R index evaluates spatial pattern at a small scale (Pielou 1969), one not likely to be affected by large-scale environment factors, the interattraction explanation is certainly credible.

Grouping on the communal threads, as measured by the R index, becomes less pronounced with time. The increase of inter-sib aggressiveness over time (Bristowe 1939), Mayer 1953, Meier 1967) or the gradual exhaustion of a spiderling's yolk reserve or both could enhance dispersal via triggering aggressive behavior; e.g., hermit crabs show heightened levels of aggression when starved (Hazlett 1966).

Meteorological factors, especially wind velocity and temperature (van Wingerden and Vugts 1974), could promote or inhibit dispersal. Variability in these factors might account for the temporal discrepancies noted by all observers between emergence from the egg sac and ballooning behavior.

On the communal web, as shown by the humidity experiments, *Araneus diadematus* spiderlings tend to spread apart at low humidities and come together at high humidities. Though such behavior appears paradoxical as regards water balance, it may represent a proper survival strategy during rainstorms. In such weather, single animals who wander or balloon away from the web could easily drown. Observations by Robinson and Robinson (1973) support this hypothesis. They noted that communal spiderlings of the orb-weaver *Nephila maculata* Fabricius, during the rainy season of New Guinea, associate into a compact ball of animals near the center of their communal structure.

How does the communal web fit as a stage in the ontogenetic development of web-building behavior? Oppenheim (1978) concludes that there are two equally important (and usually mutually exclusive) goals of ontogenetic development: the first is the gradual step-by-step building of an adult organism that can breed successfully to ensure the survival of the species (principle of developmental continuity); the second is to assure that an organism is, at each point in its development, adapted to the peculiarities of its environment (developmental discontinuity). In the second case, he emphasizes that structures or behaviors that are adaptive at one stage might be inappropriate to normal functioning in a different environment at a later stage. So, they would be suppressed, modified, or discarded altogether. Because the communal web is evidently not a training ground where spiderlings practice and gradually perfect their orb-weaving behavior, it could exemplify an adaptive discontinuity in behavioral development. In what sense might it be adaptive?

Aside from its obvious function as a substratum that economically uses available space to support a large number of animals, and its potential to increase the survivorship of grouped over isolated animals, the chief role of the communal web is probably protective

in nature. This hypothesis could be tested only negatively in the laboratory. That is, since predators were excluded under laboratory conditions, the communal web stage of development appeared less important for normal maturation. Protection against predators is the adaptive advantage of group life found in the widest diversity of animals (Wilson 1975).

In nature, the communal web is a three dimensional, radiating network, and the spiderlings typically mass into a ball-shaped configuration situated centrally within this network. Such a concentration of sensory apparatuses (Galton 1883), surrounded by filaments possessing a potential to communicate the arrival of intruders, should make the detection of predators easier. Also, collective assumption of the spheroidal configuration can effectively reduce the extent of vulnerability to enemies or adverse weather (Hamilton 1971).

The communal web period can be thought of as an interim of variable duration, giving protection to the spiderling, until optimal atmospheric conditions favor its dispersion and the construction of its first orb web.

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